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DOI: <https://doi.org/10.1017/CBO9781139044547.007>

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ZORA URL: <https://doi.org/10.5167/uzh-70529>

Book Section

Accepted Version

Originally published at:

König, Barbara; Lindholm, Anna K (2012). The complex social environment of female house mice (*Mus domesticus*). In: Macholan, Milos; Baird, Stuart J E; Munclinger, Pavel; Pialek, Jaroslav. Evolution of the House Mouse. Cambridge: Cambridge University Press, 114-134.

DOI: <https://doi.org/10.1017/CBO9781139044547.007>

The complex social environment of female house mice (*Mus domesticus*)

BARBARA KÖNIG AND ANNA K. LINDHOLM

Introduction

Conspecifics are a major environmental factor for most organisms. In sexually reproducing species they are not only mating partners, but also partners in competitive and cooperative interactions. In a social species, females therefore interact with males as potential mating partners and with other females as potential social and cooperation partners. On the other hand, conspecifics are also competitors for limited resources when living in close proximity. Conflicts are thus inevitable when females form groups, despite any benefits of group living (Alexander, 1974; Emlen and Oring, 1977; Sterck *et al.*, 1997). In recent reviews, Clutton-Brock (2009) as well as Stockley and Bro-Jørgensen (2010) emphasize the lack of knowledge about female competitive strategies, despite increasing evidence for intrasexual competition and sexual conflict among females. Female mammals regularly compete among themselves over access to resources such as food, breeding territories, nest sites, and shelter. In species with multi-female groups, they may further compete over breeding (dominance) rank, assistance with offspring care, the number of offspring raised, protection of offspring during babysitting, or social thermoregulation. Females may also compete over access to mating partners in the course of a single breeding cycle, and competitive behaviour among females generally includes aggression, weaponry, alliance formation, cooperation, and the inhibition of other females' reproduction (Rosenqvist and Berglund, 1992; Clutton-Brock, 2009; Stockley and Bro-Jørgensen, 2010). However, few data are available regarding whether differential access to resources (including mating partners) leads to differences in reproductive success, and whether social interactions affect the outcome of such reproductive competition.

The above strategies, which females may use during intrasexual competition, are less conspicuous than those used by males, and this difference has been linked to higher parental investment and lower potential reproductive rates in female

mammals (see Clutton-Brock, 2009; Stockley and Bro-Jørgensen, 2010). Nevertheless, any selective influence of reproductive competition will tend to result in the development of traits that allow for more competitive interactions. Such a process has been termed 'social selection' by West-Eberhard (1983, 1987), with sexual selection considered a subset. Social selection refers to the fact that an individual's fitness is not only determined by its own phenotype but also by the phenotype of a social partner. The potential for social selection exists whenever individual fitness varies as a result of social interactions, both in a cooperative and competitive context. In mammals in which females live in social groups, social interactions thus may provide the opportunity for the evolution of traits that improve reproductive competitiveness as well as social partner choice in females, with the prediction that interactants experience variance in fitness. So far, fitness consequences of female social interactions have only been described for primates (Silk *et al.*, 2003) and for house mice (Weidt *et al.*, 2008).

House mice are a tractable species for studies of female social interactions and female intrasexual competition, as well as the potential for reproductive competition to affect a female's social environment. Here, we first review factors that influence female–female social interactions during reproductive cooperation and competition. We then present new data from a free-living population in Switzerland showing seasonal effects on female reproductive competition and social bonding, and analyse whether differences in degree of reproductive competition and in current reproductive state affect social interactions of adult females.

Reproductive competition and cooperation in female house mice

Female house mice (*Mus domesticus*) live in social groups, and field as well as laboratory studies have illustrated their high potential for cooperation and competition over reproduction. House mice have a flexible social structure, but typically they live in small groups consisting of a dominant male, one or several adult females with their litters and several subordinate mice of both sexes (DeLong, 1967; Lidicker, 1976; Bronson, 1979; Berry, 1981; Singleton, 1983; Gray *et al.*, 2000). House mice are plural breeders, with several breeding females per group. Within groups, adult females contribute to territorial defence (Crowcroft, 1966; Latham and Mason, 2004) and cooperate in some kinds of communal care, such as babysitting, social thermoregulation, or defence of pups. The most conspicuous example of cooperation, however, is non-offspring nursing (for a review, see König, 2006). Such non-offspring nursing occurs when two – or, rarely, more – females pool their litters in a communal nest and

indiscriminately nurse both own- and non-offspring (Southwick, 1955; Sayler and Salmon, 1971; König, 1989, 1993; Manning *et al.*, 1995).

Kept under standardized conditions in the laboratory or in semi-natural enclosures, non-offspring nursing is an integral part of the reproductive behaviour of female house mice in egalitarian groups. Communal or non-offspring nursing (also referred to as allosuckling or allonursing) has been described for approximately 70 mammalian species across 12 orders, and for reproducing and non-reproducing females; nevertheless, in only 10% of such species were non-offspring nursed as much as own young, as is the case in house mice (reviewed in Packer *et al.*, 1992; Jennions and Macdonald, 1994; König, 1997, 2006; Lewis and Pusey, 1997; Solomon and French, 1997; Hayes, 2000).

Communal nursing in house mice has been studied intensively in the laboratory with direct descendants of wild-caught animals. When two females establish an egalitarian reproductive relationship, communal nursing increases both partners' individual lifetime reproductive success in comparison to females rearing litters solitarily (König, 1993, 1994a). However, the probability for such cooperation is highest when a female shares a nest with a familiar sister to form a low-skew society (König, 1994a, b, 1997, 2006). As a consequence, non-offspring nursing of female house mice in pairs with egalitarian reproduction is adaptive, and involves mutualistic direct fitness benefits. With increasing group size (three adult females per group), on the other hand, reproductive skew increases towards despotic relationships and individual reproductive success decreases below that of a solitary female. The reason why females differ in individual reproductive success as a function of group size and relatedness is that females differ in their probability to reproduce and successfully wean young within their lifetime, due to competition over reproduction, despite communal nesting and communal nursing (König, 1994a, b, 2006).

Individual fitness thus varies as a result of social interactions, and direct benefits of cooperation seem to stabilize non-offspring nursing among female house mice. Spatial proximity and nest sharing usually precede breeding associations in house mice (Manning *et al.*, 1995; Dobson *et al.*, 2000; Hayes, 2000; Rusu and Krackow, 2004), while spatial intolerance and unstable dominance relationships prior to the start of reproduction strongly impair cooperation in communal nests (Rusu and Krackow, 2004). Females may therefore be expected to carefully choose partners for subsequent breeding to avoid fitness loss, and establish social bonds to such preferred partners. In accordance with this hypothesis, female house mice display non-random preferences for social partners when kept in groups of unrelated females in semi-natural enclosures (Weidt *et al.*, 2008). Females that were afterwards allowed to live with previously preferred social partners had a higher probability to reproduce and a significantly higher lifetime reproductive success compared to females living with previously non-preferred partners. This suggests

that females generally associate with social partners with whom they have a low potential for reproductive competition (Weidt *et al.*, 2008).

In natural populations and in enclosures, female house mice spatially associate and communally nest with kin (Wilkinson and Baker, 1988; Dobson *et al.*, 2000; Dobson and Baudoin, 2002; Rusu and Krackow, 2004; Rusu *et al.*, 2004). Familiarity during juvenile development (as occurs among siblings) is of importance for such female–female social interactions (König, 1994b; D’Amato, 1997). This is in contrast to female mate choice, where dominance status (Hayashi, 1990; Drickamer, 1992) or genotypic cues (MHC complement – Yamazaki *et al.*, 1976; or *t* haplotype – Lenington and Egid, 1989) are of main relevance. This suggests that for social partner choice direct information about a potential partner’s behaviour or physiological status is more important than genetic relatedness (see also König, 1994b, 2006). Nevertheless, choosing a familiar female for social cooperation may result in close association with kin. Incidences of female competition over reproduction, mainly expressed through overt aggression, reproductive inhibition of other females or infanticide of non-offspring, on the other hand, have been typically described for unfamiliar and unrelated females (Hurst, 1987; König, 1994a; Palanza *et al.*, 1996, 2005; Rusu and Krackow, 2004).

The potential for female house mice to establish individualized social bonds among group members is therefore high. House mice mainly use odours (for a review see Stopka *et al.*, Chapter 8 in this volume), but also ultrasonic vocalizations (for review see Musolf and Penn, Chapter 10 in this volume) for intra-specific communication and individual identification, and familiar individuals can recognize each other after a separation period of at least seven days (Hurst, 1990; D’Amato, 1997; D’Amato and Moles, 2001; Nevison *et al.*, 2003).

Seasonal reproduction in house mice

Reproduction in house mice is assumed not to be obligatorily seasonal. Commensal populations usually breed all year, and feral populations breed non-seasonally in some locations, but are seasonal in others (reviewed in Latham and Mason, 2004). In his extensive review of the reproductive ecology of house mice, Bronson (1979) concluded that the interaction between caloric deprivation and the metabolic responses to cold exposure seem to be the most likely candidate for producing a seasonal interruption of the potential of mice for continuous breeding. During cold periods, reproduction is often reduced, although cold-adapted house mice have bred in frozen carcasses in deep freezer houses in the harbour of London (Laurie, 1946). Seasonal variability in commensal barn populations therefore may allow a comparison of periods with high

reproductive activity and a potentially high degree of reproductive competition, with periods of relatively low reproductive activity and thus low competition among females.

From free-living populations, however, little information is available on the social life of female house mice and how it is affected by differences in female competition over reproduction and by female bonding. Here, we illustrate the complexity of the social environment of a wild female house mouse, using new data from our long-term study of a free-living population in a barn in Switzerland. We were specifically interested in the following questions:

- Is there evidence that female reproductive competition varies seasonally?
- Does seasonality in reproductive competition affect the social environment of females?
- Does current reproductive state influence female–female social interactions independently of seasonal effects?

Assuming that (1) females display social partner preferences; (2) individual reproductive success is highest in pairs of females and decreases with increasing group size; and (3) high reproductive activity implies high reproductive competition, reproducing females are expected to choose smaller group sizes during periods of high reproductive activity.

Study population of wild house mice

Our study population was initiated in autumn 2002 by Andrea Weidt and Barbara König in a former barn, situated at the border of a forest near Illnau, Kanton Zürich, Switzerland. For a house mouse, a barn is a natural habitat. House mice in Europe occur in anthropogenic habitats, such as grain stores and farm buildings, with feral populations generally restricted to islands (Pocock *et al.*, 2004). This has been the case for a long time. Archaeological and palaeontological evidence shows that house mice were commensal with humans by 8000 BC, coinciding with new farming practices such as large-scale grain storage (Cucchi *et al.*, 2002), and that house mice colonized western Europe, commensal with humans, about 2000 years ago (Cucchi *et al.*, 2005).

Our study population was seeded with 12 wild-caught individuals, six from each of two nearby demes (altogether four males and eight females, caught at two farm houses situated within 5 km of the barn) in November 2002, and has since August 2003 been open to immigration and emigration (after successful reproduction of the founder individuals). Long-distance dispersal out of the barn occurs, as marked mice have been recovered approximately 1 km away.

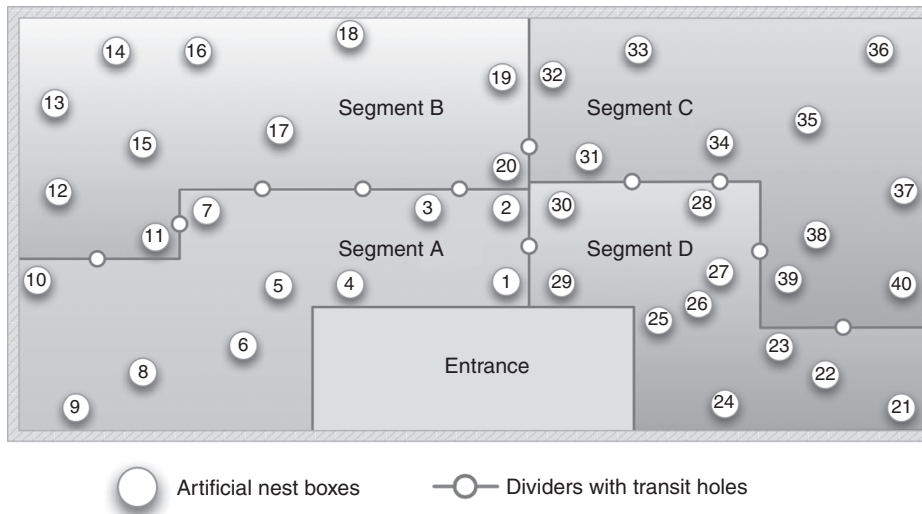


Figure 5.1 Schematic drawing of the floor of the barn (floor space 72 m²) with 40 nest boxes. Dividing walls are aluminium, 75 cm high, with 11 passages, separating the area into four quarters; next to the entrance door into the barn is a separate area for storage of equipment and for handling the mice – this is also accessible to the animals. Not shown are 2–4 feeding and drinking sites each per quarter, and further structuring of the floor with bricks and smaller wooden and plastic barriers or hides.

The barn is divided into four quarters by aluminium plates 75 cm in height, with 11 small holes allowing the passage of mice (Fig. 5.1). The floor of the barn consists of concrete, and is covered by commercial rodent bedding, and littered with bricks and wooden and plastic barriers to provide internal structure and shelters (not shown in Fig. 5.1). The mice can access all parts of the barn, and can leave it under the roof or through holes in the walls (the walls consist partly of bricks and wood). They nest in 40 artificial nest boxes (ten per quarter) and are provided with straw as nesting material. The interiors of the nest boxes are accessible to us, so offspring can be counted and measured. Food, a 50–50 mixture of oats and commercial rodent food made by Haefliger AG, is provided *ad libitum* at 9–10 feeding trays (at least two per quarter), as is water (3–4 drinking sites per quarter). Availability of food at our study site is less than would be available in grain stores and many barns, but is not limiting. We therefore consider the availability of food within the natural range. The barn itself is free of predators, but not of parasites; mice are exposed to predators, including foxes, badgers, house cats, and birds of prey, whenever they exit the barn.

Male and female mice of minimally 18 g living in the barn are implanted with a transponder (RFID tag; trovan® ID 100, 0.1 g weight, 11.5 mm length, 2.1 mm

diameter) by a trained and licensed animal care technician. Implanting transponders into smaller mice results in a high percentage of tags lost. Our method nonetheless allows tagging of all reproducing females, as no pregnant or lactating females weighing less than 19 g have been detected (2006–2010). The transponders provide a unique identity number for each mouse and a means to monitor mice remotely by transponder readers.

In 2003, 2004, and since 2006 until now, all nest boxes and shelters have been monitored weekly for the presence of tagged mice (which is done with a handheld transponder reader placed outside the nest box or a shelter) and for the presence of new litters. During 2005, monitoring was less frequent. The age of pups is estimated, and all litters are measured when they are 13 days of age (range 12–14 days; day of birth of a litter is considered as day 1). We sex the pups and take individual body weight. We refer to the number of pups at day 13 as weaning litter size, because pups are not yet mobile and thus do not mix with other litters by themselves. At 14 days of age, pups open their eyes and are mobile. They begin to eat solid food at 17 days and are weaned when 21–23 days old (dependent on litter size; smaller litters are weaned earlier; König and Markl, 1987). Offspring mortality between days 13 and 17 is almost absent in the laboratory, and we consider litter size at day 13 as a good approximation of weaning litter size also in our barn population.

In addition, at approximately seven-week intervals, comprehensive trapping has been conducted to monitor the adult population (population monitoring). Every mouse is weighed and females are examined for reproductive state (characterized as pregnant and/or lactating according to the swelling of the body and the appearance of the teats), and those adults lacking transponders are tagged. We also monitor the population for remains of deceased mice. Here, we analyse 29 population-monitoring events over a period of four years, from April 2006 until March 2010.

In May 2007 we installed permanent transponder readers in the tunnels that provide entrances to the nest boxes (two antennas per tunnel, which allows us to discriminate between a mouse entering or leaving a nest box). These readers connect to a computer and continuously track movements of tagged mice into and out of nest boxes. This provides 24-hour information on movements and social affiliations of adult mice, and makes breeding females and males easy to locate. Here we include data from 1 January 2008 to 31 December 2009 on tagged females.

Seasonal variability in reproduction

The number of adult males and females in our study population increased from an average (\pm standard error) of 29.6 ± 4.4 males (range 11–57) and 38.9 ± 3.0 females (range 27–55), respectively, in the 12 months from April 2006, to 69.7 ± 8.3 males (range 55–88) and 70.7 ± 4.8 females (40–100) in the 12

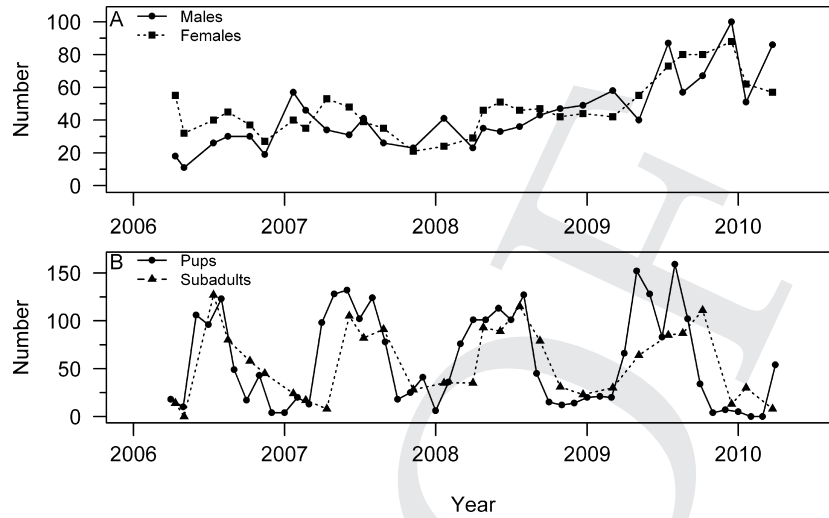


Figure 5.2 (a) Adult males and adult females (body weight at least 18 g) and (b) subadults (weaned offspring of less than 18 g) registered during population-monitoring events over a period of four years (April 2006 to March 2010; $N = 29$); (b) further shows the total number of pups sampled per month at the age of 13 days ($N = 48$).

months from April 2009 (Fig. 5.2a). No seasonal effects on adult sex ratio were obvious; however, during the first three years (2006–2008), the number of adult females was higher than the number of adult males during the summer, with the reverse effect during the winter. The number of pups weaned (13 days of age) and of subadults (weaned individuals up to a body weight of 17.5 g), on the other hand, showed marked seasonal effects, with peaks in reproductive output at 12-month intervals, during late spring/early summer (beginning April/May; Fig. 5.2b). The number of subadults registered during a single population-monitoring event reached values of up to 127 during mid-summer. Although reproduction rarely entirely stopped during the winter, it was typically drastically reduced, beginning in September/October.

Seasonality in reproduction was also reflected in the proportion of reproductive females present in the population (Fig. 5.3a). This measure may reflect female reproductive activity better than pup production, as only pups surviving to the age of 13 days are included in the latter measure. However, it may fail to include non-lactating females in early pregnancy. Generally, the proportion of females pregnant and/or lactating was lower during winter (October to March) than during summer (April to September; binomial GLM, $z_{1,27} = 9.84$, $p < 0.0001$; statistics were performed using R version 2.12.2; R Core Development Team, 2011). This is

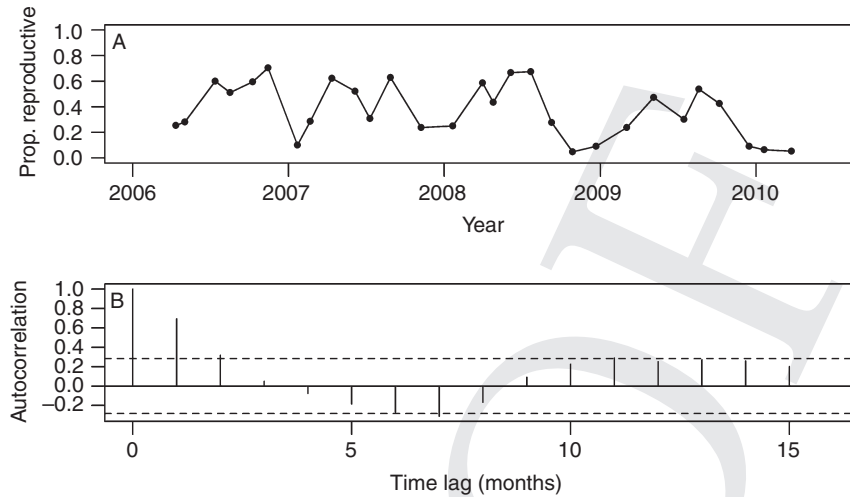


Figure 5.3 Proportion of adult females classified as reproductive (pregnant and/or lactating) during population-monitoring events; (a) over a period of four years (April 2006 to March 2010; $N=29$); (b) correlogram of temporal autocorrelation. The dashed line gives the 95% confidence interval. Vertical bars crossing the confidence interval indicate significant autocorrelations.

illustrated by the significant negative autocorrelation of the proportion of reproductively active females after a seven-month lag time (Fig. 5.3b), using linear interpolation to estimate missing monthly values (as monitoring sessions were less frequent than once per month). Peaks of positive correlations after 11–14 months indicate an approximate annual cycle in reproduction.

During the study period, the proportion of females showing reproductive activity decreased with time (binomial GLM, $z_{1,27} = 2.10$, $p < 0.05$). As numbers of adult females showed an increase with time (linear regression $t_{1,27} = 4.23$, $p < 0.001$), but numbers of reproductively active females did not (linear regression $t_{1,27} = 0.12$, $p < 0.91$), the decrease in proportion of reproductive females over time could be due to increased female competitive interactions. We used a generalized linear model to test for an effect of the number of adult females present on the proportion of females showing reproductive activity (Fig. 5.4). To remove the effect of seasonality in breeding, we averaged across 12-month intervals, and we log-transformed the average number of females present to avoid over-dispersion of errors. Indeed, reproductive activity significantly declined with increasing numbers of females present (binomial GLM, $z_{1,2} = 5.25$, $p < 0.001$).

To summarize, reproductive skew among adult females was substantial even during periods of favourable breeding conditions during summer. The number

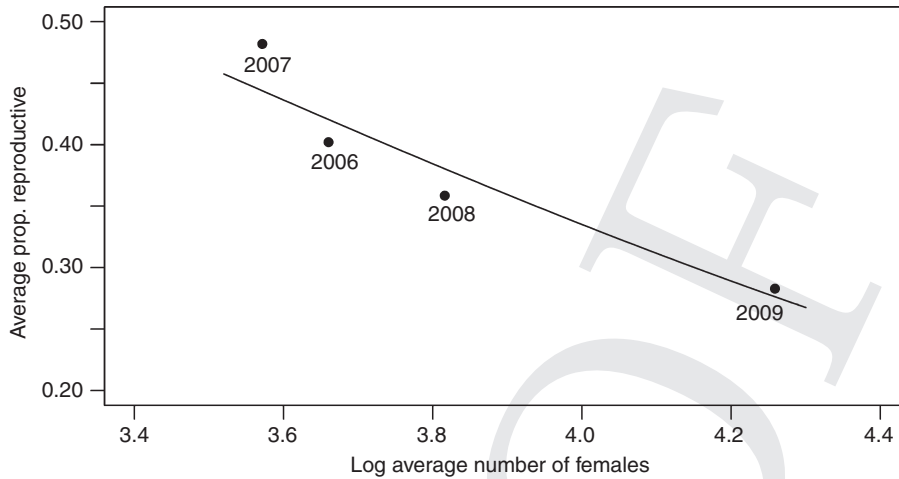


Figure 5.4 Average proportion of females classified as reproductive (pregnant and/or lactating), as a function of the log-transformed average number of females present (points), per year, with generalized linear model prediction (line).

of reproductively active females did not change significantly over the study period, nor did the annual total of pups weaned. However, the number of non-breeding adult females in the population increased over time, suggesting increasing female competition over reproduction, especially during the summer. In winter, however, under conditions of unfavourable, cold temperatures, a female's individual condition or physiology, and not necessarily reproductive competitiveness against other females, might determine whether she is able to reproduce. Reduced food and nesting material availability can be excluded in our study population as causal factors for low breeding during winter, as suggested for other wild populations (Laurie, 1946; Berry, 1968; Randall, 1999). Instead, cold and its ensuing influence on metabolism may be the greatest hazard to a female (see also Lynch, 1992).

Male condition also supports our conclusion that the strength of intrasexual selection varies seasonally. Given that wounds in males are typically inflicted during intrasexual competition over access to females, only 8.8% of adult males examined during population-monitoring events had fresh wounds on their body, head, legs, or tail in winter, but 21% were wounded during summer.

Whatever the cause of the observed seasonality in reproduction, we expect lower female competition during winter than during summer, leading to the next question of seasonal differences in female–female interactions and female bonding.

Seasonal variability in nest box use and in social interactions among females

Female nest box use and social behaviour were analysed from a two-year dataset of transponder readings in the nest boxes. For each tagged female we calculated the following monthly data (beginning with the month of tagging for females implanted after January 2008, and excluding the month during which a female died or disappeared from the barn): cumulative number of nest boxes visited; cumulative number of female partners; and cumulative number and mean duration of interactions. Social interactions and female partners were defined according to meetings in the same nest box. As soon as any two females simultaneously visited the same nest box, they were considered as partners and the meeting as a social interaction. Nest boxes are rather small, with a diameter of 15 cm, and we never observed two separate nests within one box. We therefore assume that individuals have direct contact when simultaneously visiting a box. A total of 226 females provided 1305 monthly records of such data on partners, social interactions, and number of nest boxes used.

Adult females usually met for a rather extended period of time in a nest box. An average social interaction lasted 1296 s (21.6 min), and ranged between 2 s and 4602 s (76.7 min; Fig. 5.5). A short interaction, of less than 1 min, might also be interpreted as a socio-negative or agonistic encounter, resulting in a female being chased out of the box. Substantially longer interactions between females, however, suggest a socio-positive relationship or familiarity with each other, and that

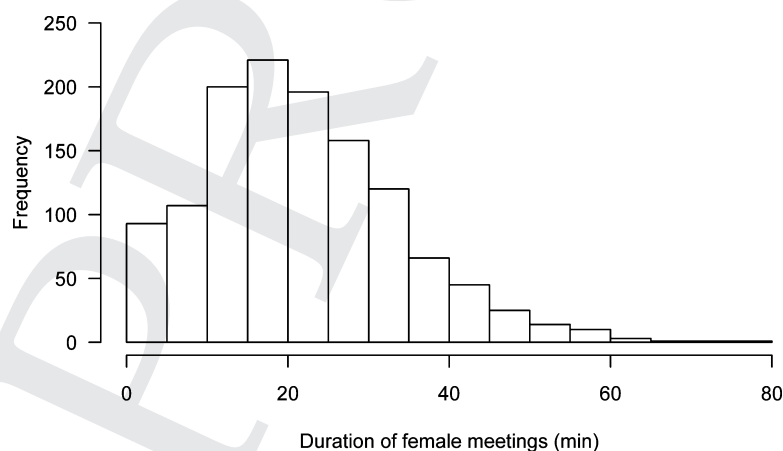


Figure 5.5 Frequency distribution of meeting duration (minutes) of any two tagged females that simultaneously visit a nest box (monthly average of the length of a female's social interactions with any other female; $N = 226$ females).

the females belong to the same social group. In 44 monthly records (5.7%), females used nest boxes without meeting another tagged female.

Influence of female reproductive state on spatial and social behaviour

In 615 monthly records, information was available on female reproductive status during that month from population-monitoring events, and was used for further analyses. We accounted for repeated measures of the same female by implementing linear mixed models in ASReml 3.0 (VSN International) with female identity as a random effect. We tested for independent and multiplicative effects of reproductive status and season on female social interactions. Accounting for repeated measures complicates determination of degrees of freedom; here, denominator degrees of freedom were calculated empirically in ASReml according to Kenward and Roger (1997).

Females differed substantially in the monthly number of nest boxes visited, which ranged between 1 and 33. Reproductively active females used fewer nest boxes than non-reproducing females (Fig. 5.6a). Furthermore, all females generally

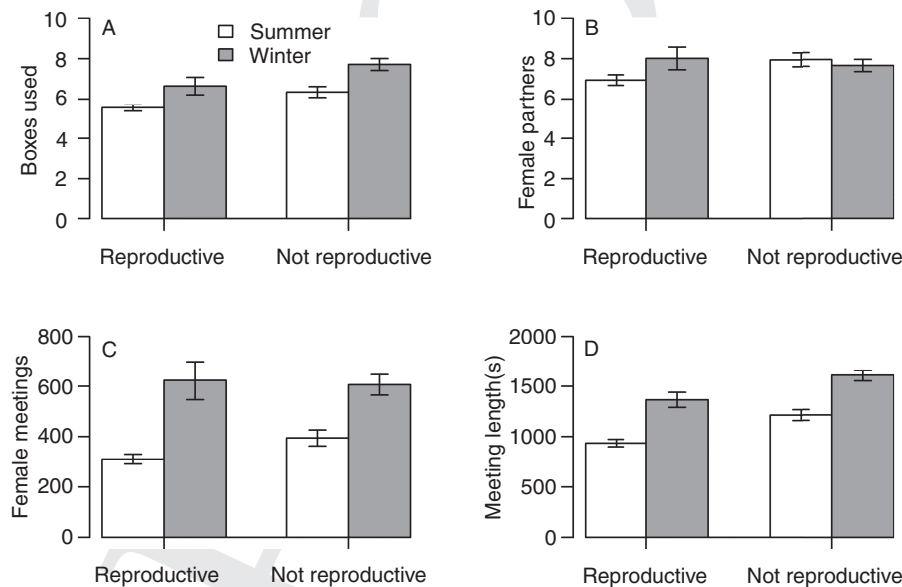


Figure 5.6 Bar plots (mean \pm SE) of monthly data on (a) cumulative number of nest boxes visited; (b) cumulative number of female partners; (c) cumulative number of female meetings; and (d) average duration of meetings, according to female reproductive status and season ($N = 615$ monthly records).

used fewer boxes in summer than in winter (reproduction: Wald statistic_{1,551} = 20.0, $p < 0.0001$; season: Wald statistic_{1,539} = 24.9, $p < 0.0001$; interaction: Wald statistic_{1,545} = 0.001, $p < 0.92$). Within nest boxes, females met with 0–19 female partners, without obvious seasonal differences (Fig. 5.6b). Nevertheless, the lowest number of partners was observed for breeding females in summer (on average 6.9 partners), with significantly fewer partners than non-reproducing females in winter (reproduction: Wald statistic_{1,488} = 3.38, $p < 0.07$; season: Wald statistic_{1,490} = 0.38, $p < 0.54$; interaction: Wald statistic_{1,491} = 8.38, $p < 0.005$).

Reproductively active females had fewer (Fig. 5.6c) and shorter meetings (Fig. 5.6d) than non-reproducing females, and during winter meetings generally were more frequent and longer than in summer (number of female meetings: reproduction: Wald statistic_{1,541} = 12.2, $p < 0.0001$; season: Wald statistic_{1,532} = 49.8, $p < 0.0001$; interaction: Wald statistic_{1,537} = 2.26, $p < 0.14$; duration of female meetings: reproduction: Wald statistic_{1,592} = 46.1, $p < 0.0001$; season: Wald statistic_{1,569} = 49.9, $p < 0.0001$; interaction: Wald statistic_{1,587} = 0.06, $p < 0.81$).

In both summer and winter females used only a limited number of nest boxes during a given month (on average 5–8 of 40 available), allowing for the conclusion that such spatial behaviour reflects an individual's home range. We have no information on female behaviour outside the nest boxes, but the rather long duration of the majority of meetings among adult females in a box suggests that partners belong to the same social group, are familiar with each other (with the potential to establish social bonds), and that all group members might contribute to defend nest boxes against non-group members (either through olfactory cues or via aggression during direct interactions; see also Hurst and Nevison, 1994).

Access to nest boxes may be a prerequisite for successful reproduction in females. The vast majority of litters in our population was born and weaned in boxes, presumably because they improve protection from disturbances by conspecifics (see also Crowcroft and Rowe, 1957, 1958; Hurst, 1987; Rusu *et al.*, 2004). Nevertheless, even reproducing females used several nest boxes and sometimes moved litters between boxes. We do not know why females regularly access several boxes even when lactating. Such behaviour can be explained by several factors, such as the option to move when faced with or disturbed by a predator, varying microclimatic needs during different environmental conditions, improved access to feeding and drinking sites, or avoidance of parasites. Since the number of partners significantly increased with the increasing number of nest boxes used (linear regression, $t_{1,1303} = 10.7$, $p < 0.0001$), at a rate of 0.32 additional partners per additional box used, larger groups may be able to defend larger

territories, which again might improve access to resources and/or defence against non-group members.

Reproductive competition nevertheless influenced the spatial and social behaviour of the females. During summer, when a higher proportion of females were breeding, reproducing females used fewer boxes than during winter, and also fewer than non-reproducing females. When radio-tracking female house mice in a feed shed, Wilkinson and Baker (1988) also observed smaller home ranges in lactating females. Reproducing females might access fewer nest boxes because they regularly nurse offspring, keep them warm, and protect them against infanticidal conspecifics, and thus have less time for exploratory behaviour. On the other hand, they are limited in the time spent with the pups, because they have to drastically increase the daily amount of food eaten to allow for milk production (König *et al.*, 1988). Still, we exclude improved access to food as a causal factor to temporarily reduce home range size during breeding in summer. First, we did not observe food storage in nest boxes, and second, in winter, when nutritional and metabolic requirements are expected to be higher than in summer, reproducing females did not show reductions in home range size. Instead, we suggest that reproducing females under conditions suggesting high reproductive competition are more restrictive in access to social partners. As predicted from previous lab studies, they meet with relatively few partners, despite the fact that relatively more other females are breeding. Highly pregnant or lactating females might be more choosy in terms of with whom they meet, as preferences for social partners result in low conflicts over reproduction and improved offspring survival (see Weidt *et al.*, 2008). Furthermore, under experimental lab conditions individual lifetime reproductive success decreases with increasing number of females (König, 2006), and it has been shown for other rodents and larger mammals that female competition increases with increasing group size (reviewed in Silk, 2007).

Adult females rarely stayed in a nest box in the absence of any other adult female, suggesting that meetings in social groups and established social bonds play an important role in reproductive success. Social partners may serve various functions for a reproducing female. If the social partner is also lactating, both can establish a communal nest and gain mutual benefits through cooperative nursing of litters. During summer, on the other hand, relatively many non-reproducing adult females were also observed in our population. Social bonds to a non-reproducing female might allow a lactating female to gain benefits through helping to improve protection of offspring, social thermoregulation, or even allonursing by non-reproducing females.

Future analyses of fitness benefits arising from individual associations between reproducing and non-reproducing females in our study population will help us to

understand how the presence of other females influences individual reproductive success. If benefits of communal or cooperative care of young are substantial, we then predict that reproducing females are especially choosy with respect to social partners, and restrict interactions to only a few other reproducing females in order to maximize reproductive success (König, 1994a).

Presumably as a consequence of having fewer partners, reproducing females had fewer meetings during summer. In addition, they had shorter meetings in summer, the period of elevated reproductive competition. Such behaviour might suggest that breeding females alternated in their presence in the nest with other females, and minimized the time of simultaneous nest use. Alternating with other females reduces the time litters are left alone and are thus unprotected during periods of high energetic demand of the mother. Such a benefit would be obvious, especially for communally nursing females, and in captivity wild females have been observed to take turns nursing each other's offspring in communal nests (Wilkinson and Baker, 1988; König, 1989).

In winter, females had more partners, more meetings, and longer meetings than during summer, irrespective of their reproductive condition. Females thus decreased the time outside of nest boxes, presumably to minimize exposure to low temperatures in winter. In addition, larger groups may provide thermoregulatory benefits. Huddling as a social strategy against low temperature is widespread among rodents, and several otherwise solitary species nest communally during the winter, thereby reducing exposure to the environment and consequent heat loss (Martin *et al.*, 1980; Batchelder *et al.*, 1982; McShea, 1990; Hayes, 2000). The absence, or only weak presence, of reproductive competition during winter might have relaxed the reproducing females' selectivity in interactions with other group members, and thus allowed for the observed large number of partners. In African striped mice (*Rhabdomys pumilio*), a strictly seasonal breeder, reproductive competition even favours solitary living. After the breeding season, in the absence of reproductive competition, almost all striped mice live in groups even under very low population densities. During the breeding season, however, mice of both sexes may live solitarily, except under very high population density, when no opportunities for independent breeding exist (Schradin *et al.*, 2011; 2011).

Conclusions

Our free-living study population of house mice in northern Switzerland showed distinct seasonality in female reproductive activity over a period of four years, despite unlimited access to food, water, and protected nesting sites. Such seasonality had interesting consequences for female reproductive competition and the quality of female–female interactions. During summer (April to

September), intrasexual competition among females was pronounced, and might explain why only a limited number of females were able to reproduce in the well-established population. Although population size and the number of adult females increased over the study period, the absolute number of reproductively active females remained unchanged. During winter (October to March), the proportion of reproducing females and the monthly number of offspring weaned were much lower, suggesting relaxed reproductive competition. It is unlikely that female house mice competed strongly over access to mates, since the number of adult males to adult females was rather equal over the entire period. They rather seemed to compete over resource availability, in particular access to nest boxes as a prerequisite to rear and protect a litter. Only when females drastically outnumber males or simultaneously share mate preferences, female competition may also encompass access to mates, as has been suggested by Rusu and Krackow (2004).

Throughout the year, females used a variety of nest boxes where they regularly interacted with several reproducing and adult non-reproducing female conspecifics belonging to the same social group. Despite the fact that analysis of long-term stability in interaction partners is still lacking, such a pattern underlines the significance of same-sex social partners and individualized social groups. Average life expectancy in the study population is 196 days, but adult females can live up to three or four years (Manser *et al.*, 2011). Very interestingly, generation time (average age of reproduction of a female), at nine months, is surprisingly long (Manser *et al.*, 2011), suggesting that especially younger females need to integrate and establish long-term social bonds within a group as a prerequisite to successfully wean offspring. Our long-term data thus propose that females maintain social bonds to other females even during periods of low reproductive competition, as part of a flexible and competitively superior reproductive strategy.

Within groups, social relationships appear to be structured by cooperation and by the existence and resolution of conflicts. During summer, when intrasexual competition was high, reproductively active females had relatively few partners and used few nest boxes. Limitation of lactating females' access to social partners is expected according to laboratory data, since individual reproductive success is highest for communally nursing pairs of females, and decreases with increasing group size (König, 2006). During winter, on the other hand, reproductive competition was low and the benefits of social thermoregulation might outweigh the benefits of reducing the number of social partners.

Theory predicts that the aversive effect of reproductive competition could be offset by kin association. Even when reproductive skew occurs within social groups, the long-term inclusive fitness of interacting females, when related, should then be higher than of females not exhibiting social preferences. Within social groups, female house mice have the option to establish preferences and

restrict meetings to fewer partners when reproducing under conditions of high intrasexual competition. Genetic relatedness among interacting partners has still to be analysed for our free-living population, as well as whether individual preferences result in fitness variances. Nevertheless, female social behaviour has to be interpreted in the context of long-term relationships and such relationships are typically complex. Interactions among females thus may be subject to social selection processes, driving the evolution of female traits. Future studies have to analyse whether females choose social partners based on their phenotype, to identify the traits they use for partner preferences, and whether social selection results in assortative traits of social partners.

REFERENCES

- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, **5**, 325–83.
- Batchelder, P., Kinney, R. O., Demlow, L., and Lynch, C. B. (1982). Effects of temperature and social interactions on huddling behaviour in *Mus musculus*. *Physiology and Behavior*, **31**, 97–102.
- Berry, R. J. (1968). The ecology of an island population of the house mouse. *Journal of Animal Ecology*, **37**, 445–70.
- Berry, R. J. (1981). Town mouse, country mouse: adaptation and adaptability in *Mus domesticus* (*M. musculus domesticus*). *Mammal Review*, **11**, 91–136.
- Bronson, F. H. (1979). The reproductive ecology of the house mouse. *The Quarterly Review of Biology*, **54**, 265–99.
- Clutton-Brock, T. H. (2009). Sexual selection in females. *Animal Behaviour*, **77**, 3–11.
- Crowcroft, P. (1966). *Mice All Over*. London: GT Foulis & Co.
- Crowcroft, P. and Rowe, F. P. (1957). The growth of confined colonies of the wild house mouse (*Mus musculus* L.). *Proceedings of the Zoological Society of London*, **129**, 359–70.
- Crowcroft, P. and Rowe, F. P. (1958). The growth of confined colonies of the wild house-mouse (*Mus musculus* L.): the effect of dispersal on female fecundity. *Proceedings of the Zoological Society of London*, **131**, 357–65.
- Cucchi, T., Vigne, J.-D., and Auffray, J.-C. (2005). First occurrence of the house mouse (*Mus musculus domesticus* Schwarz, 1943) in the Western Mediterranean: a zooarchaeological revision of subfossil occurrences. *Biological Journal of the Linnean Society*, **84**, 429–45.
- Cucchi, T., Vigne, J.-D., Auffray, J.-C., Croft, P., and Peltenburg, E. (2002). Passive transport of the house mouse (*Mus musculus domesticus*) to Cyprus at the Early Preceramic Neolithic (late 9th and 8th millennia cal. BC). *Comptes Rendus Palevol*, **1**, 235–41.
- D'Amato, F. R. (1997). Neurobiological and behavioral aspects of recognition in female mice. *Physiology Behavior*, **62**, 1311–17.

- D'Amato, F. R. and Moles, A. (2001). Ultrasonic vocalizations as an index of social memory in female mice. *Behavioral Neuroscience*, **115**, 834–40.
- DeLong, K. T. (1967). Population ecology of feral house mice. *Ecology*, **48**, 611–34.
- Dobson, F. W. and Baudoin, C. (2002). Experimental tests of spatial association and kinship in monogamous mice (*Mus spicilegus*) and polygynous mice (*Mus musculus domesticus*). *Canadian Journal of Zoology*, **80**, 980–6.
- Dobson, F. W., Jacquot, C., and Baudoin, C. (2000). An experimental test of kin association in the house mouse. *Canadian Journal of Zoology*, **78**, 1806–12.
- Drickamer, L. C. (1992). Oestrous female house mice discriminate dominant from subordinate males and sons of dominant from sons of subordinate males by odour cues. *Animal Behaviour*, **43**, 868–70.
- Emlen, S. T. and Oring, L. W. (1977). Ecology, sexual selection, and evolution of mating systems. *Science*, **197**, 215–23.
- Gray, S. J., Jensen, S. P. and Hurst, J. L. (2000). Structural complexity of territories: effects on preference, use of space and territorial defence in commensal house mice (*Mus domesticus*). *Animal Behaviour*, **60**, 765–72.
- Hayashi, S. (1990). Social condition influences sexual attractiveness of dominant male mice. *Zoological Science*, **7**, 889–94.
- Hayes, L. D. (2000). To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour*, **59**, 677–88.
- Hurst, J. L. (1987). Behavioural variation in wild house mice *Mus domesticus* Ratty: a quantitative assessment of female social organization. *Animal Behaviour*, **35**, 1846–57.
- Hurst, J. L. (1990). Urine marking in populations of wild house mice *Mus domesticus* Ratty: II – communication between females. *Animal Behaviour*, **40**: 223–32.
- Hurst, J. L. and Nevison, C. M. (1994). Do female house mice, *Mus domesticus*, regulate their exposure to reproductive priming pheromones? *Animal Behaviour*, **48**, 945–59.
- Jennions, M. D. and Macdonald, D. W. (1994). Cooperative breeding in mammals. *Trends in Ecology and Evolution*, **9**, 89–93.
- Kenward, M. G. and Roger, J. H. (1997). The precision of fixed effects estimates from restricted maximum likelihood. *Biometrics*, **53**, 983–97.
- König, B. (1989). Behavioural ecology of kin recognition in house mice. *Ethology, Ecology Evolution*, **1**, 99–110.
- König, B. (1993). Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). *Behavioural Processes*, **30**, 611–74.
- König, B. (1994a). Components of lifetime reproductive success in communally and solitarily nursing house mice: a laboratory study. *Behavioral Ecology and Sociobiology*, **34**, 275–83.
- König, B. (1994b). Fitness effects of communal rearing in house mice: the role of relatedness and familiarity. *Animal Behaviour*, **48**, 1149–57.
- König, B. (1997). Cooperative care of young in mammals. *Naturwissenschaften*, **84**, 95–104.
- König, B. (2006). Non-offspring nursing in mammals: general implications from a case study on house mice. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. P. M. Kappeler and van C. P. Schaik. Berlin, Heidelberg: Springer-Verlag, pp. 191–205.

- König, B. and Markl, H. (1987). Maternal care in house mice: I – the weaning strategy as a means for parental manipulation of offspring quality. *Behavioral Ecology and Sociobiology*, **20**, 1–9.
- König, B., Riester, J., and Markl, H. (1988). Maternal care in house mice (*Mus musculus*): II – the energy cost of lactation as a function of litter size. *Journal of Zoology*, **216**, 195–210.
- Latham, N. and Mason, G. (2004). From house mouse to mouse house: the behavioural biology of free-living *Mus musculus* and its implications in the laboratory. *Applied Animal Behaviour Science*, **86**, 261–89.
- Laurie, E. M. O. (1946). The reproduction of the house mouse (*Mus musculus*) living in different environmental conditions. *Proceedings of the Royal Society B: Biological Sciences*, **133**, 248–81.
- Lenington, S. and Egid, K. (1989). Environmental influences on the preferences of wild female house mice for males of differing *t*-complex genotypes. *Behavior Genetics*, **19**, 257–66.
- Lewis, S. E. and Pusey, A. E. (1997). Factors influencing the occurrence of communal care in plural breeding mammals. In *Cooperative Breeding in Mammals*, ed. N. G. Solomon and J. A. French. Cambridge: Cambridge University Press, pp. 335–63.
- Lidicker, W. Z., Jr (1976). Social behaviour and density regulation in house mice living in large enclosures. *Journal of Animal Ecology*, **45**, 677–97.
- Lynch, C. B. (1992). Clinal variation in cold adaptation in *Mus domesticus*: verification of predictions from laboratory populations. *The American Naturalist*, **139**, 1219–36.
- Manning, C. J., Dewsbury, D. A., Wakeland, E. K., and Potts, W. K. (1995). Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour*, **50**, 741–51.
- Manser, A., Lindholm, A. K., König, B., and Bagheri, H. (2011). Polyandry and the decrease of a selfish genetic element in a wild house mouse population. *Evolution*, **65**, 2435–47.
- Martin, R. A., Fiorentini, M., and Connors, F. (1980). Social facilitation of reduced oxygen consumption in *Mus musculus* and *Meriones unguiculatus*. *Comparative Biochemistry and Physiology*, **65A**, 519–22.
- McShea, W. J. (1990). Social tolerance and proximate mechanisms of dispersal among winter groups of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, **39**, 346–51.
- Nevison, C. M., Armstrong, S., Beynon, R. J., Humphries, R. E., and Hurst, J. L. (2003). The ownership signature in mouse scent marks is inviolate. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1957–63.
- Packer, C., Lewis, S., and Pusey, A. E. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour*, **43**, 265–82.
- Palanza, P., Della Seta, D., Ferrari, P. F., and Parmigiani, S. (2005). Female competition in wild house mice depends upon timing of female/male settlement and kinship between females. *Animal Behaviour*, **69**, 1259–71.
- Palanza, P., Re, L., Mainardi, D., Brain, P. F., and Parmigiani, S. (1996). Male and female competitive strategies of wild house mice pairs (*Mus musculus domesticus*) confronted with intruders of different sex and age in artificial territories. *Behaviour*, **133**, 863–82.

- Pocock, M. J. O., Searle, J. B., and White, P. C. L. (2004). Adaptations of animals to commensal habitats: population dynamics of house mice *Mus musculus domesticus* on farms. *Journal of Animal Ecology*, **73**, 878–88.
- Randall, J. A. (1999). *Vertebrate Pest Management: A Guide for Commercial Applicators*. East Lansing, MI: Michigan State University.
- R Core Development Team (2011). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rosenqvist, G. and Berglund, A. (1992). Is female sexual behaviour a neglected topic? *Trends in Ecology and Evolution*, **7**, 174–6.
- Rusu, A. S., König, B., and Krackow, S. (2004). Pre-reproductive alliance formation in female wild house mice (*Mus domesticus*): the effects of familiarity and age disparity. *Acta Ethologica*, **6**, 53–8.
- Rusu, A. S. and Krackow, S. (2004). Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice. *Behavioral Ecology and Sociobiology*, **56**, 298–305.
- Sayler, A. and Salmon, M. (1971). An ethological analysis of communal nursing by the house mouse. *Behaviour*, **40**, 60–85.
- Schradin, C., König, B., and Pillay, N. (2011). Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*, doi 10.1111/j.1365-294X.2011.05256.x.
- Schradin, C., Lindholm, A. K., Johannesen, J., et al. (2011). Social flexibility as a tool to understand social behaviour. *Molecular Ecology*. In press.
- Silk, J. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 539–59.
- Silk, J., Alberts, S. C., and Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231–4.
- Singleton, G. R. (1983). The social and genetic structure of a natural colony of house mice, *Mus musculus*, at Healesville Wildlife Sanctuary. *Australian Journal of Zoology*, **31**, 155–66.
- Solomon, N. G. and French, J. A. (1997). *Cooperative Breeding in Mammals*. Cambridge: Cambridge University Press.
- Southwick, C. H. (1955). Regulatory mechanisms of house mouse populations: social behavior affecting litter survival. *Ecology*, **36**, 627–34.
- Sterck, E. H. M., Watts, D. P., and van Schaik, A. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, **41**, 291–309.
- Stockley, P. and Bro-Jørgensen, J. (2010). Female competition and its evolutionary consequences in mammals. *Biological Reviews*, **86**, 341–66.
- Weidt, A., Hofmann, S. E., and König, B. (2008). Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Animal Behaviour*, **75**, 801–8.
- West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *The Quarterly Review of Biology*, **58**, 155–83.
- West-Eberhard, M. J. (1987). Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249–78.

- Wilkinson, G. S. and Baker, A. E. M. (1988). Communal nesting among genetically similar house mice. *Ethology*, **77**, 103–14.
- Yamazaki, K., Boyse, E. A., Miké, V., *et al.* (1976). Control of mating preferences in mice by genes in the major histocompatibility complex. *Journal of Experimental Medicine*, **144**, 1324–35.